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Feeding ecology in the natural world

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Introduction

Foraging mode, originally defined on the basis of clear differences in behaviors used to find and capture prey (MacArthur and Pianka, 1966; Pianka, 1966; Schoener, 1971) has become a central paradigm in lizard ecology (see, for example, Huey and Pianka, 1981; Vitt and Congdon, 1978; Cooper, 1994a,b, 1995a,b; Perry, 1999; Perry and Pianka, 1997; Perry *et al.*, 1990). Sit-and-wait (often referred to as "ambush") foragers pursue prey detected visually from short distances, often returning to the same perch after capturing a prey item. Wide (often referred to as "active") foragers move through the environment in search of prey that are often hidden, using a combination of visual and chemical cues to locate and discriminate prey. Trade-offs between energy invested in capture versus search for these two foraging modes are key elements of optimal foraging theory (MacArthur and Pianka, 1966; Charnov, 1976; Kamil, 1983). Identification of this foraging dichotomy has stimulated lizard research in many areas, including ecology, behavior, life histories, and physiology, to mention a few.

The foraging mode paradigm is much more complex than previously envisioned, as evidenced by research presented in other chapters in this book. For example, what appeared to be a sharp historical separation of foraging modes (see, for example, Pianka and Vitt, 2003; Vitt *et al.*, 2003) is replete with exceptions embedded in major clades, suggesting either loss of or multiple origins of traits often linked to foraging mode (see, for example, Cooper, 1997; Cooper *et al.*, 1997). Empirical data on components of foraging mode (e.g. percent time moving) also reveal a much more complex pattern (Perry, 1999; this volume, Chapter 1). Prey detection systems (visual versus olfactory) (Cooper *et al.*, 1997; Schwenk, 1995, 2000a,b), jaw function (Schwenk, 2000b; McBrayer and Reilly, 2002), behavior (Anderson and Karasov, 1981; Anderson and Vitt, 1990), and even thermal physiology are associated loosely with

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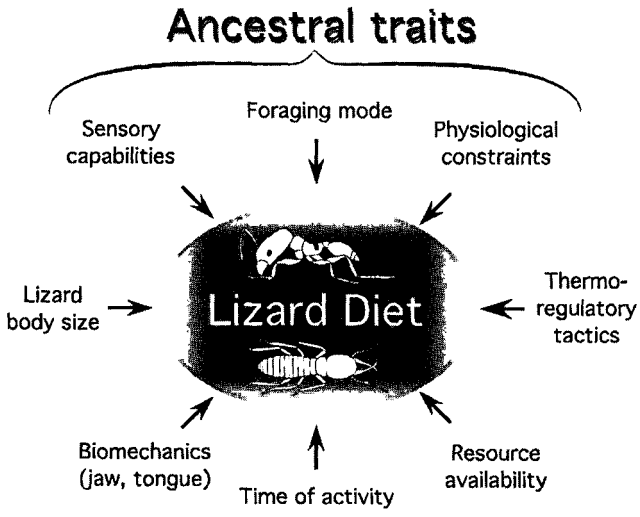

Figure 5.1. Possible sources of variation in lizard diets.

foraging mode but not necessarily predictable based exclusively on variation in foraging behavior.

We comment on major evolutionary and non-evolutionary factors that affect the kinds of prey eaten by lizards. We use data from our combined studies on lizards conducted in African, Australian, and North American deserts by ERP and the New World Tropics by LJV. Specifically, we comment on eight factors that appear *a priori* most likely to influence lizard diets: lizard body size, biomechanics of feeding structures, thermoregulatory tactics, time of activity, sensory capabilities, physiological constraints, foraging mode, and resource availability, all of which are constrained by phylogeny either directly or indirectly (Fig. 5.1). Clearly, these are not independent and the relative impact of each on the others remains largely unstudied. We comment on this as well. Finally, and most importantly, we emphasize earlier analyses (Vitt *et al.*, 2003; Vitt and Pianka, 2005) that show that a large portion of differences in diets among lizard clades is historical, and likely tied to several key events in the evolutionary history of sensory systems and differential involvement of the tongue and jaws in prey prehension.

Prior to addressing each of these, a comment on the nature of dietary data is necessary. Most lizards eat a diversity of invertebrates, along with some plant material (see, for example, Cooper and Vitt, 2002). Some species feed primarily on leafy vegetation (e.g. Iguanidae) (Iverson, 1979; Durtsche, 2000; Espinoza *et al.*, 2004), some are specialists on specific invertebrates (e.g. some tropidurids, phrynosomatids, and agamids specialize on ants) (Vitt and Zani, 1996a; Vitt *et al.*, 1997; Pianka and Parker, 1975; Pianka and Pianka 1970), while still

others feed primarily on other vertebrates (e.g. *Lialis*, *Heloderma*, and most varanids) (Auffenberg, 1978; Shine, 1986; Beck, 1990; Beck and Lowe, 1991; Pianka, 1994; Pianka and King, 2004). Many other lizard species have very broad diets. Unlike many other kinds of data, dietary data are extremely complex. Size of prey eaten by an individual lizard over a period of time or by a population of lizards at one time consists of a distribution that is usually log-normal and a set of taxonomic categories varying in both frequency and size. Thus no single number can easily be assigned as representative of a particular species' diet. Moreover, for some lizard species, diets vary considerably as a function of availability of prey as evidenced by seasonal and spatial variation in diets (see, for example, Sexton *et al.*, 1972; Dunham, 1980; Vitt, 1991; Miranda and Andrade, 2003; Rocha, 1996; Van Wyk, 2000; Pianka, 1970; Vitt and Colli, 1994), whereas for other species, diets vary little from time to time or geographically (e.g. *Phrynosoma*: Pianka and Parker, 1975; Sherbrooke, 1981 or *Plica umbra*: Vitt *et al.*, 1997). Complicating dietary data even further is the observation that diets sometimes change ontogenetically (see, for example, Mautz and Nagy, 1987; Durtsche *et al.*, 1997; Durtsche 2000).

Finally, a comment is necessary on evolutionary patterns of prey prehension in squamates, because two hypotheses exist. One (McBrayer and Reilly, 2002; Reilly and McBrayer, this volume, Chapter 10) maintains that squamate ancestors possessed both lingual and jaw prehension and thus both are ancestral. Reilly and McBrayer (this volume, Chapter 10) use that argument as a basis for concluding that "lingual prehension" in some skinks is primitive retention rather than a functional reversal, even though the few skinks in which this has been observed are deeply nested within clades using jaw prehension. Wagner and Schwenk (2000) and Schwenk (2000b) consider obligate lingual prehension ancestral and obligate jaw prehension derived in scleroglossans with loss of lingual prehension associated with use of the tongue for other functions (e.g. cleaning in gekkotans and chemical sampling in autarchoglossans). Even though some iguanians use their jaws to pick up unusually large prey (e.g. *Crotaphytus* and *Gambelia*), this is not the obligate jaw prehension observed in scleroglossans, the tongue is involved, and insectivorous iguanians rarely eat large prey (see Vitt *et al.*, 2003). To us, the evidence summarized by Schwenk's (2000b) arguments is much more compelling and provides a more parsimonious view of the evolution of prey prehension in squamates. Use of tongues in prey capture in highly derived skinks, for example, more likely represents reversals, and the underlying lingual mechanism is most certainly different from that found in iguanians. For this chapter, we follow Schwenk (2000b) and leave the continuing debate to functional

morphologists. However, when we return to historical (phylogenetic) factors affecting lizard diets, we re-examine some of our earlier conclusions in the context of a very different and provocative new view of squamate evolution (Townsend *et al.*, 2004).

Methods

Methods for collection of lizards and identification and measurements of prey appear elsewhere (see, for example, Pianka, 1973, 1986; Vitt and Zani, 1996b). We consider both prey sizes and types in our analyses, noting that they likely are not entirely independent. Because prey sizes were log-normally distributed, data were $\log_{10}$ transformed prior to statistical tests. We then compared prey size among target groups (foraging modes, clades, etc.) with an ANOVA. These analyses fail to account for differences in sample sizes among species or potential effects of lizard body size on prey size. To adjust for differences in prey size associated with lizard body size, we calculated mean body size (snout–vent length, SVL) and mean prey size for all lizard species, $\log_{10}$-transformed the variables, and conducted analyses of covariance (ANCOVA) with SVL as the covariate.

We briefly comment on some changes we made to our original datasets. Initial prey categories for desert and neotropical lizards were nearly identical, which allows us to re-analyze our data at various taxonomic levels. The original neotropical lizard data set included 30 broad prey types, whereas the original desert lizard data set included 20 broad prey types. Some more detailed dietary datasets for desert lizards are also available. Relatively few prey categories accounted for most of the diets of all lizards included. We specifically selected data on target species to make points in our discussion of factors affecting lizard diets. Thus, our examples, by design, in some cases represent extremes. Earlier, we combined data to come up with generalized diets for specific cladès (Pianka and Vitt, 2003; Vitt *et al.*, 2003). In doing so, we restricted our analysis to mean percent utilization by volume of the seven most important prey categories for all lizards: ants (A), beetles (B), grasshoppers and crickets (G), non-ant hymenopterans (H), insect larvae, pupae, and eggs (L), spiders (S), and termites (T). Ants were treated as a unique category (rather than including them with other hymenopterans) because they exhibit their own morphotype, are highly diverse and abundant, and because some lizards specialize on them (i.e. lizards discriminate ants from other hymenopterans).

Finally, to reconstruct the history of dietary change in lizards, we combined our datasets and constructed a large data matrix consisting of diets of 184 species using 27 prey categories. These data constituted the dependent variable.

The independent variable was the clade representation of each species. Because lizard size affects diet and covaries with clade, average lizard species snout–vent length was entered as a covariate (see Vitt and Pianka, 2005). We discovered an error in dietary data for one species (*Anolis n. scypheus*) that we had overlooked in a previous analysis (Vitt and Pianka, 2005) and corrected it. We applied a canonical phylogenetic ordination based on Canonical Correspondence Analysis (CCA) (Giannini, 2003), a multivariate ordination procedure that directly associates variation in one matrix (lizard diets in this case) to variation in another (lizard phylogeny in this case). Thus, in this analysis, we ask whether an association exists between dietary composition and identified divergence points in the evolutionary history of lizards (see Vitt and Pianka, 2005 for detailed methods). The CCA was performed with CANOCO 4.5 (Ter Braak and Smilauer, 2002). We used symmetric scaling and unimodal methods and downweighted rare prey categories. In a stepwise procedure, each variable was then tested by using 9999 Monte Carlo permutations to obtain F and p values. After each significant variable was included in the model, the subsequent variable that most reduced variance was tested and included if statistically significant ($p < 0.05$). This procedure was followed until subsequent variables were no longer significant.

Lizard body size

In general, larger lizards eat larger prey (Fig. 5.2). However, much remains hidden in such regressions. On a purely statistical basis, the relation between

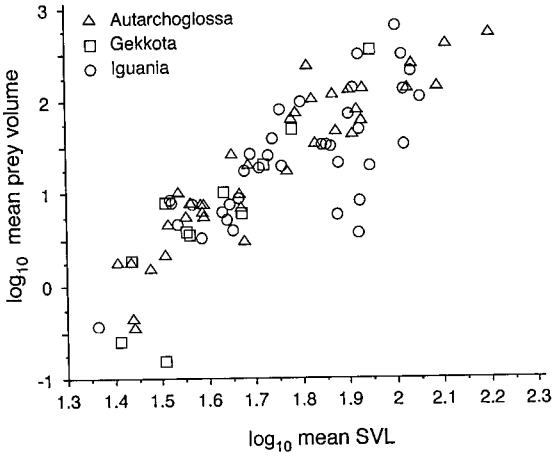

Figure 5.2. Relation between lizard mean body size (snout–vent length) and mean prey size for neotropical lizards. Each point represents a lizard species.

Table 5.1 *ANCOVAs with log_{10} mean SVL as the covariate, clade level as the class variable, and log_{10} mean prey volume as the dependent variable*

We retained full effects in analyses in which interaction terms were insignificant ($p > 0.05$) because interaction terms were marginally significant. Xantusiidae and Anguidae were removed from the third (family-level) analysis because each was represented by a single species. Clades are in order of mean prey size (largest to smallest).

	Slope test		Intercept	
Clades used	*F* value	*p* value	*F* value	*p* value
Iguania, Scleroglossa (1, 1, 82)	3.89	0.0521	4.49	0.0654
Iguania, Gekkota, Autarchoglossa (1, 2, 80)	3.95	0.0231	162.74	< 0.0001
Teiid, Scinc, Iguan, Gekk, Gymno (4, 4, 74)	2.39	0.0585	113.39	< 0.0001

prey size and lizard size varies among higher- and lower-level clades (Table 5.1). Reasons underlying this relationship are complex. We point to a few here and return to more later on in this chapter.

Lizards that are "generalists" (e.g. *Ameiva ameiva*) tend to eat a wide variety of prey sizes, and prey size is often associated with lizard size (Fig. 5.3) such that their diet usually consists of many small prey items and some large ones. Most likely, head size (as it affects gape) and biomechanics of the jaw and food processing structures limits the absolute size of prey that can be eaten. However, exactly what determines the maximum prey size that a lizard can take remains unclear. Lizards can eat some unusually large prey volumetrically if they are long and narrow. For example, a *Sceloporus clarkii* might eat a centipede (*Scolopendra heros*) longer than its body that completely fills its stomach, but it may not be able to eat a scarab beetle with a mass of only one third that of the centipede. Individual prey volume or length may not be the best measures of prey size when considering potential constraints on maximum prey size. For the few lizards that dismember their prey (e.g. *Varanus komodoensis*) (Auffenberg, 1978, 1981), no measures of prey size are relevant; rather, the size of the piece that the lizard can swallow determines size of portions.

Prey size of lizards that are dietary specialists (e.g. *Plica umbra*) appears to vary considerably less and is not associated with lizard body size, or at least to a lesser degree (Fig. 5.3). Ant-specialized lizards (e.g. *Moloch*, *Phrynosoma*, *Phrynocephalus*, *Plica*) tend to have broad, short heads and eat prey that are very small relative to the lizard's head. Length of the epipterygoid bone and to a lesser degree, vertical diameter of the mandible in the skull of horned lizards are negatively associated with percent of ants in the diet, suggesting that

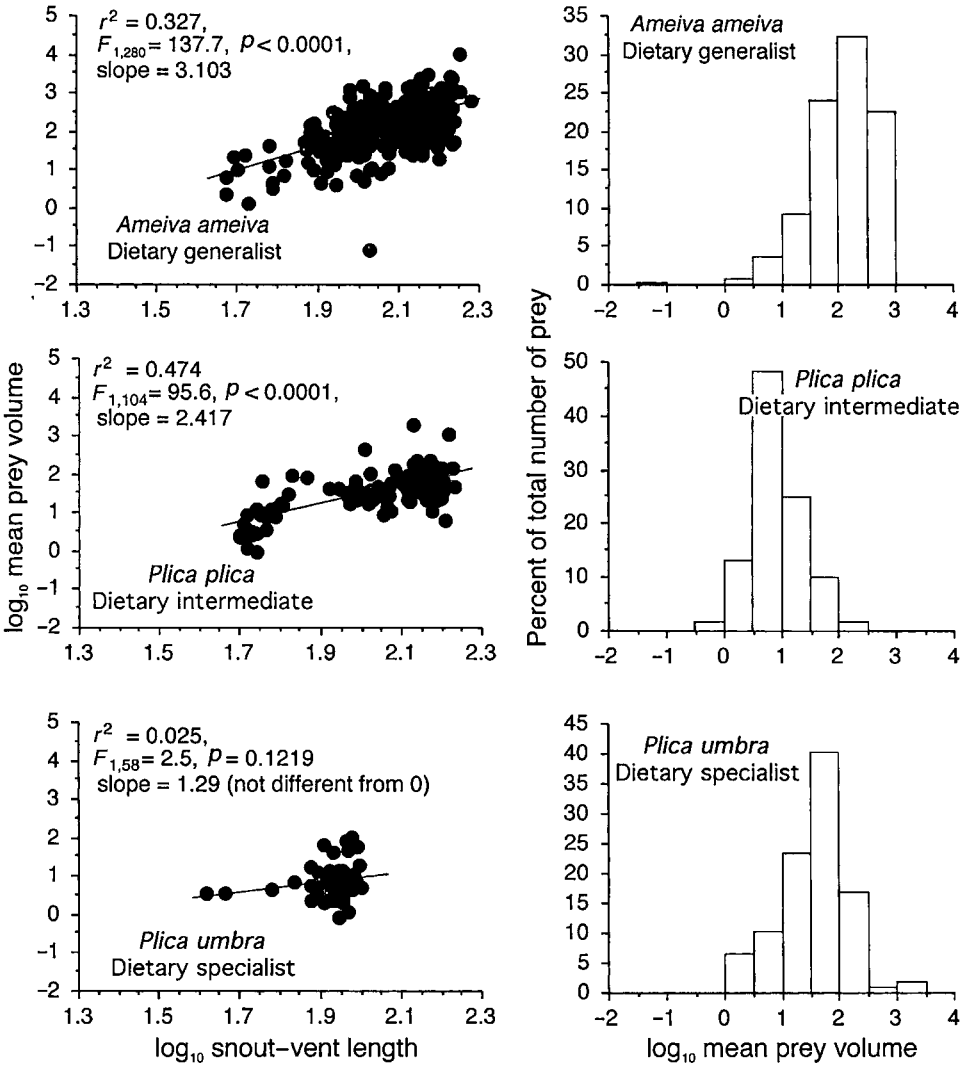

Figure 5.3. Relation between individual lizard snout–vent length and mean prey size for a dietary specialist (*Plica umbra*), a generalist (*Ameiva ameiva*), and a species with an intermediate diet (*Plica plica*).

morphological change in skull morphology results from specialization on ants (Montanucci, 1989). It might be particularly instructive to examine convergences (if any) in feeding mechanics of these unrelated lizards to determine whether apparent convergence in head morphology is associated with dietary specialization: why should a short, broad head be good for eating ants, and do the same skull modifications occur in ant-eating clades other than *Phrynosoma*? Most likely, underlying skull modifications are modifications

in mechanics of tongue extension for capturing ants. If true, then one has to ask how teiids, lacertids, geckos, and skinks that eat large numbers of termites (also small relative to lizard head size) effectively ingest these small prey without lingual prehension.

Even though large lizards on average eat larger prey than smaller ones, prey size does not scale directly with lizard body or head size. As an example, consider the range of prey sizes eaten by the large, actively foraging teiid lizard *Ameiva ameiva* (Fig. 5.3). *Ameiva* of all sizes eat a lot of small prey, but large ones can and do eat a few prey that are much larger than those eaten by smaller *Ameiva*. Figure 5.3 shows only mean prey size for each individual, such that inclusion of many small prey is not apparent. If prey size scaled directly with body size, the slope of the regression lines should approach 3.0 (volume scales geometrically with length). For both *Ameiva* and *P. plica*, slopes of lines are considerably flatter than that. Failure of prey size to scale directly with lizard size may simply reflect the fact that most insects (a majority of the diet of *Ameiva* and *P. plica*) are small, so most lizards, particularly moderate to large-bodied species, do not have the option of selecting just a few large prey if they are to maintain positive energy balance. Varanids, helodermatids, *Lialis*, and snakes have shifted to unusually large prey by extreme modifications of the jaw and skull, modification or loss of the pectoral girdle (including limb loss), or dismemberment of unusually large prey (some varanids).

Biomechanics of feeding structures

The biomechanics of lizard feeding are just beginning to be examined experimentally (McBrayer and Reilly, 2002; Reilly and McBrayer, this volume, Chapter 10), and we suspect that experiments using kinds and sizes of prey similar to those eaten in nature will be most illuminating. The greatest challenge facing studies of feeding mechanics is demonstrating that morphological and functional variation affect observed differences in diets among species. To be convincing, such studies must be performed with natural prey of each lizard species. Differences among lizard species in the ability to manipulate and ingest prey that are well outside of the size range, of a different consistency, or of taxa different from those of naturally eaten prey are irrelevant.

As a group, squamates eat a remarkable diversity of prey types. Community ecologists divide prey into morphotypes to compare diets of species (see, for example, Pianka, 1973, 1986). Such categorization, useful in ecology, may not be best for studies of functional morphology. Lizards that use lingual prehension might be able to ingest any dry solid prey item of suitable size but unable to ingest a prey item with a highly flexible and damp body (e.g. an earthworm

or pulmonate) (K. Schwenk, pers. comm.). Nevertheless, some Amazonian iguanians include earthworms in their diets (e.g. *Enyalioides* and some *Anolis* species). Lizards using jaw prehension can not only pick up such prey, they can use their snouts to root through surface debris and capture many hidden insect larvae as well as other invertebrates and small vertebrates (Vitt and Cooper, 1986). Moreover, jaw prehension allows a lizard to capture large prey, some of which are killed by rapid thrashing of the prey against rocks and other surface items. If jaw and tongue mechanics evolved in squamates in response to changes in diets (as opposed to diets changing in response to changes in jaw or lingual structure tied to something else), then diets of clades differing in jaw and tongue structure and use should differ in a predictable manner based on underlying jaw and tongue structure and function.

Dietary differences are apparent among major clades (Vitt and Pianka, 2005). The most obvious example of an association between feeding structure biomechanics and diet is in snakes, which have evolved a jaw structure accommodating ingestion of large prey relative to snake head size (Greene, 1997). Although members of one snake clade (Scolecophidia) have relatively rigid skulls with positioning of the quadrate and size of the supratemporal and mandible more or less similar to anguimorphan ancestors, higher snakes (alethinophidians) have various degrees of posterior migration of the quadrate, enlargement and extension of the supratemporal, loose mandibular symphysis, elongation of the mandible to accommodate ingestion of large prey, and independent movement of left and right maxillae (Cundall and Greene, 2000). These modifications, combined with loss of a pectoral girdle, accommodate a shift to vertebrates as primary prey. However, among lower-level clades (e.g. families within clades), dietary differences may not correlate with differences in feeding structures.

Within squamates typically referred to as "lizards," the most apparent difference in prey observed at the Iguania–Scleroglossa divergence is the drastic reduction in ants, other hymenopterans, and beetles in scleroglossan diets (Vitt and Pianka, 2005). Three non-exclusive hypotheses exist to explain this shift: (1) use of olfactory (Gekkota) and volmerofactory (Autarchoglossa) cues allowed scleroglossans to selectively eliminate prey producing noxious chemicals (particularly alkaloids) from their diets; (2) chemoreception in scleroglossans allowed them to discriminate prey quality, resulting in selection of prey of potentially higher energy content (Pianka and Vitt, 2003; Vitt *et al.*, 2003); and (3) the switch to jaw prehension resulted from a switch to larger prey (Schwenk, 2000b). Our data do not support hypothesis 3. Support exists for the first two hypotheses and they share common elements. Nevertheless, reasons for differences remain largely unexplored.

Thermoregulatory tactics and time of activity

Thermoregulatory tactics have not been examined with reference to squamate diets. Nevertheless, lizard species vary considerably in body temperatures while active, and different species are active at different times. The most extreme variation exists between diurnal and nocturnal squamates, which for lizards, breaks down phylogenetically (most gekkonids are nocturnal, but most other lizards are diurnal). However, considerable temperature variation exists between lizards that seek direct sun to elevate their body temperatures (thermoregulators, heliotherms) versus those that maintain most activity in shaded environments such that their body temperatures remain similar to low temperatures in shade (thermoconformers). Active body temperatures also vary between and within lizard clades. For example, among Teioidea, lacertids and teiids are active thermoregulators with relatively high body temperatures, whereas gymnophthalmids in rainforest have substantially lower body temperatures and appear to be thermoconformers (Vitt and Pianka, 2004).

Comparison of nocturnal versus diurnal lizard diets reveals the obvious: nocturnal lizards feed on more nocturnal insects, such as crickets, moths, and certain spiders, than do diurnal lizards (see Parker and Pianka, 1974; Pianka and Pianka, 1976; Avery, 1981; Doughty and Shine, 1995; Vitt, 1995; Vitt and Zani, 1997). Differences in resource availability between night and day offer the best explanation for such dietary differences. However, behavior of some nocturnal geckos suggest that maintenance of higher body temperatures during the day than those experienced at night may increase digestion rates and possibly facilitate other metabolic processes (Autumn *et al.*, 1999; Huey *et al.*, 1989). An Australian gecko, *Christinus marmoratus*, for example, thermoregulates by positioning itself in crevices and achieves relatively high body temperatures during the day (Kearney and Predavec, 2000). Similarly, behavioral thermoregulation increases growth rates in another gecko (Autumn and DeNardo, 1995).

Herbivorous lizards face the challenge of digesting plant materials that contain cellulose, often accomplished by microflora-induced gut fermentation (Troyer, 1984; Durtsche, 2000). Most studied herbivorous lizards are either active at higher body temperatures (e.g. *Dipsosaurus*; Pianka, 1971) or have extended activity to accommodate nutritional assimilation (Zimmerman and Tracy, 1989; van Marken Lichtenbelt, 1992; Vitt *et al.*, 2005). Small-bodied herbivorous lizards in the southern Andes appear to operate at lower body temperatures (Espinoza *et al.*, 2004), and it remains to be seen whether they compensate by increasing activity periods (see Vitt, 2004).

Sensory capabilities

Gekkotans use visual cues for detecting prey but also discriminate prey chemically via the nasal olfactory system. Autarchoglossans use both visual and chemical cues for locating prey, and they discriminate prey based on heavy non-volatile chemicals. The impact of these differences in sensory abilities on lizard diets is profound. For autarchoglossans, the ability to detect prey by means other than visual cues made available to them a huge diversity of insect taxa and life history stages not harvested to a significant degree by iguanians, including, but not limited to, termites, beetle larvae, cryptic insects and spiders, aquatic insects, mollusks, and hidden vertebrates (Vitt and Pianka, 2005). Coupled with jaw prehension (*sensu* Schwenk, 2000b), it also allowed some autarchoglossans to find, capture, and subdue large and in some instances potentially dangerous prey, such as those used by varanoid lizards and large teiids. Jaw prehension combined with serrated teeth in some varanids expanded dietary opportunities even more, allowing some species to kill prey much too large to ingest intact and later to dismember dead prey and swallow it in pieces (e.g. *Varanus komodoensis*; Auffenberg, 1981).

The most obvious effect of sensory capabilities on diet is the reduction of insects that use chemical defenses observed in the Scleroglossa. Ants, other hymenopterans, and beetles are less prevalent in scleroglossan diets. Development of an acute nasal olfactory system in gekkotans and an acute vomeronasal chemical sensing system in autarchoglossans provided opportunities for scleroglossans to discriminate among prey types based on chemical signals (see, for example, Cooper, 1994a,b, 1995b; Cooper and Hartdegen, 1999). Whether scleroglossans actively avoid beetles, ants, and other hymenopterans because they contain chemicals that might interfere with metabolic processes or whether they simply select prey with higher energy content remains uncertain. However, experiments on autarchoglossan responses to chemicals suggest the former (Cooper *et al.*, 2002a,b).

Physiological constraints

Physiological constraints on diet include phenomena such as differences between insectivorous and herbivorous lizards in relative stomach volume as well as gut length and anatomy (Ostrom, 1963; Iverson, 1982). However, without question, temperature is the primary physiological constraint on lizard diets. Body temperature has a major impact on all physiological processes because lizards are ectothermic poikilotherms (Huey, 1982). Not only do many lizards have relatively low body temperatures, but even those with

high body temperatures experience hourly, daily, and seasonal variation in body temperatures. Effects of temperature related to feeding in squamates include foraging (Wilhoft, 1958; Ayers and Shine, 1997), hunger (Alexander *et al.*, 2001), efficiency of capturing and handling prey (Greenwald, 1971; de Queiroz *et al.*, 1987), efficiency of absorption (Harlow *et al.*, 1976; Harwood, 1979; Beaupre *et al.*, 1993), regulation of vitamin production (Ferguson *et al.*, 2003), transport of nutrients to tissues via circulation, assimilation efficiency (Ballinger and Holscher, 1980; Troyer, 1987; Xue-Feng *et al.*, 2001), specific dynamic action (Zaidan and Beaupre, 2003), overall metabolic rates (Zimmerman and Tracy, 1989; van Marken Lichtenbelt and Wesselingh, 1993; Spotila and Standora, 1985; but see Nussear *et al.*, 1998 for a counter example), and assimilation of preformed water (Kaufmann and Pough, 1982; Clarke and Nicolson, 1994).

An as yet unexplored constraint to foraging and behavior in general is the potential effect of alkaloid intake in the diet as the result of hymenopteran and beetle consumption. These insects are well known to contain alkaloids (Blum, 1981). Reduction in intake of insects containing alkaloids associated with the shift from visual to chemosensory prey discrimination (see Pianka and Vitt, 2003; Vitt *et al.*, 2003) at the Iguania–Scleroglossa transition released scleroglossans from effects of alkaloids on metabolic processes. Appropriate physiological studies to verify this are needed.

Foraging mode

As discussed above, foraging mode influences types of prey a lizard encounters. Sit-and-wait foragers hunt visually and hence only encounter mobile prey as they move past ambush stations, whereas widely foraging predators encounter more potential food items as well as a wider variety, because they search for hidden and sedentary prey (Huey and Pianka, 1981). Analyzing lizard diets strictly in the context of foraging mode presents a number of problems. First, foraging mode is strongly correlated with phylogeny, although some reversions have occurred. Almost without exception, iguanians ambush their prey, whereas most autarchoglossans forage widely (Cordylidae and a few Varanidae have reverted back to the ancestral sit-and-wait mode of foraging). Geckos have been variously classified, both as sit-and-wait ambush foragers, and as active widely foraging predators. Underlying the association of foraging mode with phylogeny are dramatic shifts in prey detection and handling between iguanians, gekkotans, and autarchoglossans. Some dietary differences associated with foraging mode are to be expected, but foraging mode may not be the primary cause of these differences (see below).

Resource availability

Effects of resource availability on lizard diets are complex. On the one hand, if competition accounts for some of the structure in lizard assemblages, then food resources may be limiting. However, whether resource levels measured by sticky traps, pitfalls, or any other methods bear directly on actual resource availability to lizards remains to be seen. In risky environments (high predator diversity or abundance), measured resources could be very high, but risks involved in acquiring those resources might be so high that effectively some resources are unavailable to lizards.

Many people naively assert that lizards are opportunistic feeders, eating whatever is available in their environment. If this were true, all lizards living together in an area would eat the same prey in the same proportions. This is manifestly not the case: dietary differences among species are the rule rather than the exception (see, for example, Pianka 1973, 1986; Vitt and Zani, 1996b). Nevertheless, for many species, diets vary with seasons as pointed out earlier. Within assemblages, dietary differences among species are maintained in spite of seasonal or annual variation in diets (see, for example, Vitt, 1991). Some species, however, are specialists, feeding on just a few prey categories to the exclusion of others, regardless of time of year or locality. Various species of lizard have specialized on ants, termites, scorpions, and large vertebrate prey. For example, ant specialization has evolved independently in agamids (*Phrynocephalus* and *Moloch*: Anderson, 1999; Pianka and Pianka, 1970; Pianka *et al.*, 1998), phrynosomatids (*Phrynosoma*: Pianka and Parker, 1975; Sherbrooke, 1981), and tropidurids (*Plica* and *Uracentron*: Vitt *et al.*, 1997; Vitt and Zani, 1996a) to mention a few. Termite specialization has evolved in scincids (*Typhlosaurus*: Huey *et al.*, 1974; *Ctenotus*: Pianka, 1969), lacertids (*Heliobolus*, *Pedioplanus*: Pianka, 1986), and gekkonids (*Diplodactylus*: Pianka and Pianka, 1976; *Pachydactylus*: Pianka and Huey, 1978; Pianka, 1986). The diurnal Kalahari lacertid *Nucras tessellata* and the nocturnal Australian pygopodid *Pygopus nigriceps* are scorpion specialists (Pianka, 1986). Another pygopodid, *Lialis burtonis*, preys almost exclusively on vertebrates, especially skinks. Monitor lizards of the genus *Varanus* and teiids in the genus *Tupinambis* also specialize on large vertebrate prey, in Australia and the neotropics, respectively.

As an example of interactions among foraging mode, time of activity, and resource availability, consider Australian termite specialist geckos and skinks (Huey *et al.*, 2001). Australian geckos are nocturnal sit-and-wait foragers, whereas sympatric skinks are diurnal and forage widely. These dietary specialists show striking variation in feeding success. More than 50% of all stomachs of three gecko dietary specialists were empty (*Diplodactylus conspicillatus*,

D. pulcher, *Rhynchoedura ornata*) (Pianka and Pianka, 1976; Pianka, 1986). Several sympatric Australian *Ctenotus* skink species that specialize on termites have substantially lower frequencies of empty stomachs: *C. ariadnae* 20%, *C. grandis* 6.4%, *C. pantherinus* 12.4% (Huey *et al.*, 2001). Diurnal WF termite specialists capture termites in their tunnels, in termitaria, or in open foraging trails, and would appear to have more reliable access to termites than nocturnal SW species, which must capture termites at night when these insects are active above ground. Termite activity at night appears to be unreliable (certainly termite swarms are).

Rather than there being a single vector of resource availability that applies to all species, instead each species experiences its own unique vector of resource availability, which is an outcome of the interaction between its perceptual abilities, body size, time of activity (daily and seasonal), use of space (microhabitat and habitat), as well as its foraging mode and thermoregulatory tactics (thermoconformer–thermoregulator). Because it would be difficult, if not impossible, to estimate such a unique resource availability vector for each species (utilization is much easier to estimate than "availability"), we have to seek other ways to analyze dietary differences among species. One useful way is to sum the diets of all lizards living together in a particular place and to use this as a bioassay of what foods are available to lizards at that locality (Winemiller and Pianka, 1990). Then, dietary utilization of each prey type by each species can be expressed as "electivities" (Ivlev, 1961) that reflect the degree to which each species uses each resource disproportionately to its relative abundance (as used by all species). Electivities can be scaled from -1 to $+1$, with -1 representing complete avoidance of a prey type and $+1$ complete specialization on a given prey type in which no other species eats that prey category. Alternatively, electivities can be scaled from 0 to 1, with 0.5 representing random utilization, numbers below 0.5 representing avoidance, and numbers above 0.5 representing positive selection of a given prey type.

Proportional utilization coefficients are heavily biased towards abundant resources, and thus tend to overestimate dietary similarity, whereas electivities give greater weight to scarce resources and better reflect dietary niche segregation (Winemiller and Pianka, 1990). These differences are rather dramatic when proportional utilization coefficients are compared with electivities in a tropical assemblage of Nicaraguan lizards (Fig. 5.4). The Winemiller and Pianka (1990) community analysis uses geometric means (g_i) of electivities (e_i) and proportional utilization coefficients (p_i) to reduce bias. Surprisingly, the "same" analysis in the ecological analytical software package Ecosim (Gotelli and Entsminger, 2004) uses only p_i data, thus producing results biased toward abundant resources.

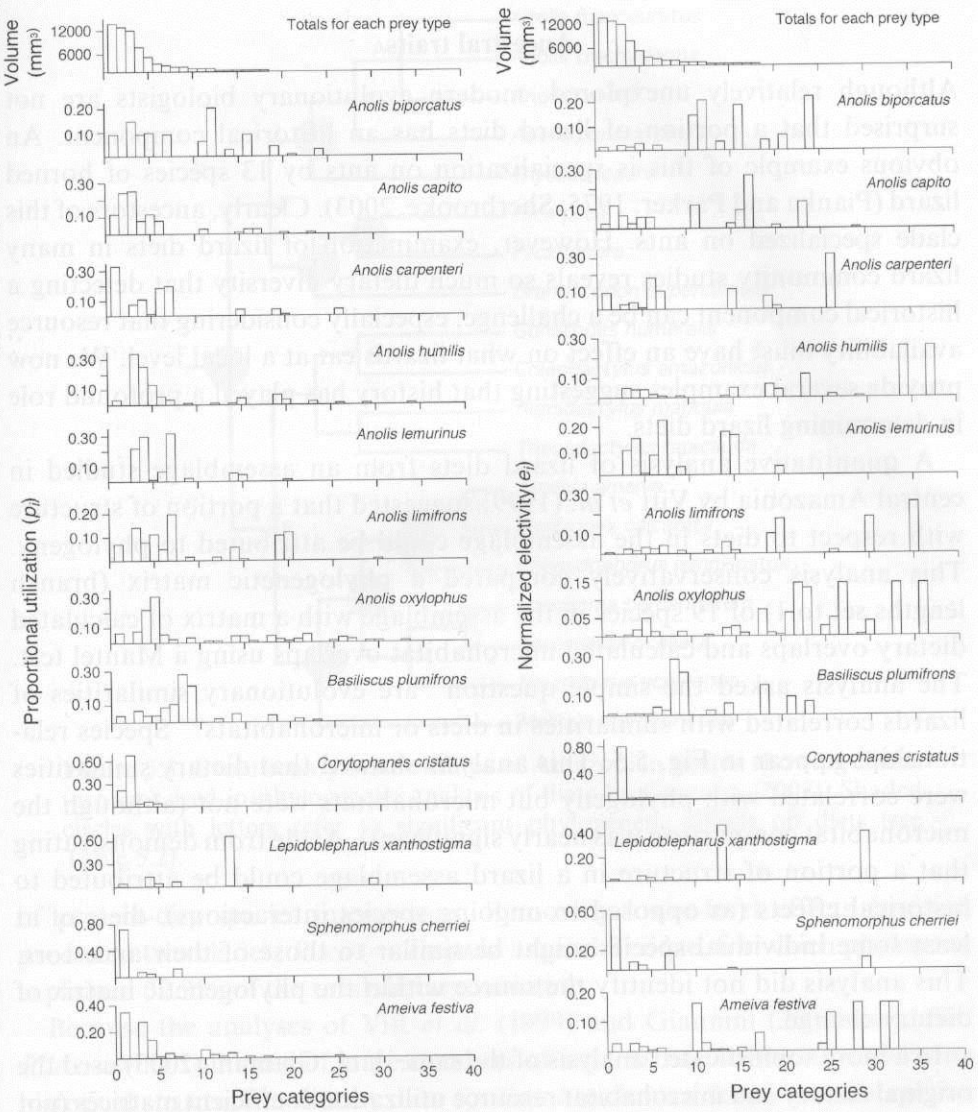

Figure 5.4. Differences between dietary data expressed as proportional utilization coefficients (p_i) and electivities (e_i). The 37 prey categories, from left to right, are: roaches, cicadas, grasshoppers and crickets, spiders, insect larvae, beetles, homopterans, fruit, hymenopterans, walking sticks, hemipterans, frogs, ants, lepidopterans, millipedes, lizards, lizard eggs, lizard shed skin, crustaceans, isopods, dragonflies, mantids, centipedes, phalangids, mollusks, flies, earthworms, scorpions, collembolans, termites, leeches, thysanurans, earwigs, pseudoscorpions, trichopterans, psocopterans, and mites (from Vitt and Zani, 1998).

Ancestral traits

Although relatively unexplored, modern evolutionary biologists are not surprised that a portion of lizard diets has an historical component. An obvious example of this is specialization on ants by 13 species of horned lizard (Pianka and Parker, 1975; Sherbrooke, 2003). Clearly, ancestors of this clade specialized on ants. However, examination of lizard diets in many lizard community studies reveals so much dietary diversity that detecting a historical component can be a challenge, especially considering that resource availability must have an effect on what lizards eat at a local level. We now provide several examples suggesting that history has played a profound role in determining lizard diets.

A quantitative analysis of lizard diets from an assemblage studied in central Amazonia by Vitt *et al.* (1999) suggested that a portion of structure with respect to diets in the assemblage could be attributed to phylogeny. This analysis conservatively compared a phylogenetic matrix (branch lengths set to 1) of 19 species in the assemblage with a matrix of calculated dietary overlaps and calculated microhabitat overlaps using a Mantel test. The analysis asked the simple question "are evolutionary similarities of lizards correlated with similarities in diets or microhabitats?" Species relationships appear in Fig. 5.5. This analysis showed that dietary similarities were correlated with phylogeny but microhabitats were not (although the microhabitat comparison was nearly significant). Aside from demonstrating that a portion of structure in a lizard assemblage could be attributed to historical effects (as opposed to ongoing species interactions), diets of at least some individual species might be similar to those of their ancestors. This analysis did not identify the source within the phylogenetic matrix of dietary change.

In a more sophisticated analysis of the same data, Giannini (2003) used the original dietary and microhabitat resource utilization coefficient matrices (not overlaps) and a phylogenetic matrix maintaining all monophyletic group structure (as opposed to similarities among species pairs) to tease out underlying historical effects on diets and microhabitat use. A canonical correspondence analysis (CCA) was applied to compare matrices using Monte Carlo methods to estimate statistical significance. The dietary portion of the analysis revealed significant phylogenetic effects for 7 of 15 comparisons (Table 5.2) shown as shaded circles on Fig. 5.5. Dietary divergence has occurred at several levels within the phylogeny, supporting the hypothesis that dietary differences among species might affect their relative abilities to exist in present-day communities and can have a history largely independent

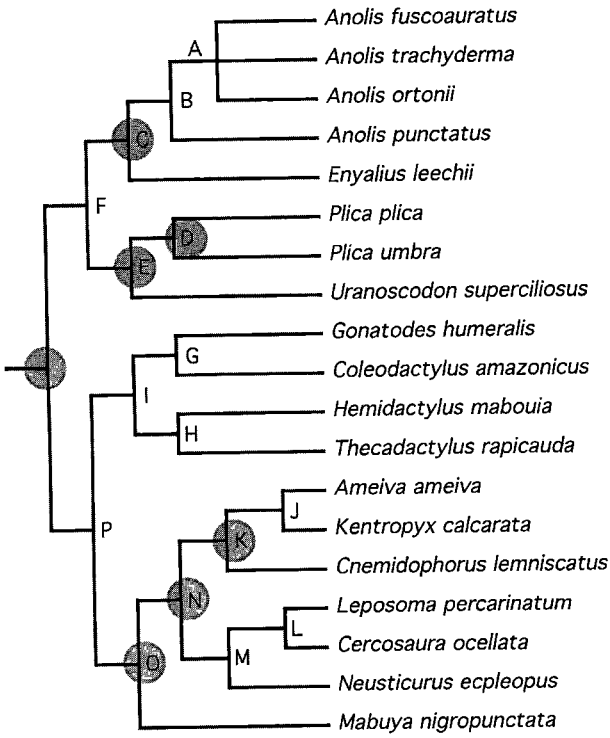

Figure 5.5. Evolutionary relationships of Amazonian lizards showing clades (groups) used in phylogenetic analysis of diets by Giannini (2003). Shaded circles with letters refer to significant phylogenetic effects on diets (see Table 5.2).

of present-day species interactions. Removing lower-level effects (species) produced two clades, *Plica* (= *Tropidurus*) and Teiidae, for which phylogeny explained 32.3% of the total dietary variation.

Because the analyses of Vitt *et al.* (1999) and Giannini (2003) identified *Plica*, owing to its use of large numbers of ants, as one source of underlying historical structure in dietary data for this Amazonian lizard assemblage, we take a closer look at its evolutionary history. Within the clade Tropiduridae, the Amazonian lizard *Uranoscodon superciliosus* is the sister taxon to the clade containing *Tropidurus*, *Plica*, and *Uracentron* (Frost, 1992) (Fig. 5.6). This lizard lives along streams and lagoons where it feeds on a variety of invertebrates, many of which are taken from waterway edges and may actually float up in the water (Howland *et al.*, 1990). The sister taxon contains a history of divergence centered in open cerrados of Brazil with reinvasion of arboreal microhabitats in rainforest of the Amazon and Orinoco River basins (Fig. 5.6). *Tropidurus* in open areas eat large numbers of ants, but volumetrically ants do not dominate their diets. *Plica* and *Uracentron* eat mostly ants, and at least

Table 5.2 *Historical effects on diet of Amazonian lizards*

Groups are monophyletic clades depicted in Fig. 5.5. Variation is the percent variation explained by each identified clade with F statistic and p values resulting a canonical correspondence analysis with a reduced tree matrix from 999 permutations of a Monte Carlo analysis on the original phylogenetic hypothesis. The first seven groups are significant (underlined).

Group (s)	Variation	F	p
D	22.1	4.8	0.001
F/P	16.6	3.4	0.001
K	14.4	2.9	0.002
O	14.3	2.8	0.006
E	14.2	2.8	0.013
N	14.1	2.8	0.011
C	11.4	2.2	0.042
J	7.7	1.4	0.279
I	5.9	1.1	0.380
H	5.9	1.1	0.390
B	4.2	0.7	0.565
G	2.4	0.4	0.596
M	1.6	0.3	0.884
A	1.3	0.2	0.918
L	0.3	0.1	0.982

Source: Table 1 in Giannini (2003).

Uracentron flaviceps and *Plica umbra* are ant specialists. Thus the tropidurid ancestor to the clade containing *Plica* and *Uracentron* likely had a diet consisting largely of ants. More importantly, the tendency toward ant-eating evolved in ancestors living in open habitats (Brazilian cerrado), not Amazonian rainforest, even though *Plica* and *Uracentron* are strictly rainforest species today.

To examine possible historical effects more closely, we performed a comparable canonical phylogenetic ordination on our combined neotropical and desert lizard dataset with more prey categories (Vitt and Pianka, 2005). Diets for 184 lizard species were summarized based on 27 prey categories: larvae/eggs/pupae, vertebrates, ants, beetles, centipedes, earthworms, earwigs, flies, grasshoppers/crickets, non-ant hymenopterans, isopods, lepidopterans, mantids/phasmids, millipedes, miscellaneous insects, mites, mollusks, odonates, harvesters, plants, psocopterans, roaches, scorpions, spiders, springtails, termites, and bugs (Hemiptera + Homoptera). We used proportional utilization data based on volumes of prey (electivities could not be used because they

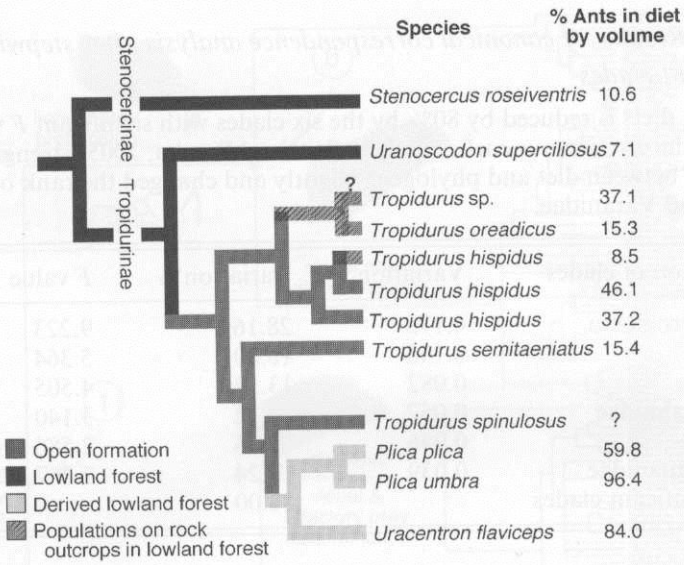

Figure 5.6. Relationships of tropidurid lizards showing the phylogenetic distribution of ant-eating in the clade.

must be based on lizard assemblages). We examined phylogenetic effects at the family and higher taxonomic category levels. Variation was significant in 14 of the 19 taxonomic groups (Vitt and Pianka, 2005). However, because residual variation changes with the inclusion of each clade, only 6 of the 14 remained significant in the final overall model (Table 5.3). Significant dietary shifts at these six major divergence points reduced variation in diets by a full 80.0%. Clearly, phylogenetic effects on lizard diets are profound. These results confirm the findings of Vitt *et al.* (2003) and identify numerous sources of dietary variation within the evolutionary history of lizards (Fig. 5.7). Unfortunately, there was a minor error in one line of the 184 in Vitt and Pianka (2005). Here, we present corrected results, which differ slightly from those reported earlier: Figure 5.8A is a biplot showing the position of each prey category in dietary niche space (prey types that are eaten together are close to each other on this plot, whereas those that are seldom eaten by the same lizard species are far apart). The origin at 0.0, 0.0 represents the lowest common denominator or the overall lizard diet summed across all 184 species. Vectors show positions of clades that significantly reduced residual variation in diet. Iguania and Scleroglossa vectors are diametrically opposed: iguanians prey heavily on ants, other Hymenoptera, beetles, and bugs. Agamids and iguanids are relatively close together in the lower left quadrant. However, scleroglossans are scattered around the other three quadrants. Scleroglossans consume a wide range of prey, with skinks feeding on termites and varanids on spiders

Table 5.3 *Results of canonical correspondence analysis after stepwise inclusion of significant clades*

Variation in diets is reduced by 80% by the six clades with significant F values. Correcting the error in our earlier dataset (Vitt and Pianka, 2005) strengthened the relationship between diet and phylogeny slightly and changed the rank order of Scincidae and Varanidae.

After inclusion of clades	Variation	Variation%	F value	p value
Iguania/Scleroglossa	0.176	28.16	9.223	0.0001
Varanidae	0.100	16.00	5.364	0.0001
Scincidae	0.082	13.12	4.505	0.0001
Gymnophthalmidae	0.057	9.12	3.140	0.0003
Teiidae	0.046	7.36	2.586	0.0034
Agamidae/Iguanidae	0.039	6.24	2.207	0.0168
Total of significant clades		80.00		

and vertebrates. Teiids and gymnophthalmids consume orthopterans and centipedes. This graph shows that scleroglossans eat many prey items rarely consumed by iguanians. Moreover, scleroglossans feed on prey types arranged at right angles to iguanian vectors (Fig. 5.8B). The shaded area in Fig. 5.8B corresponds to the area in Fig. 5.8A. Species are spread out in dietary niche space more than clades, which represent sets of species. Dietary generalists with broad food niches lie in the interior of the plot near the origin, and specialists are on peripheral areas of the diagram. We interpret these results as showing how acquisition of chemical prey discrimination, jaw prehension, and wide foraging opened up a new food resource base for scleroglossans, providing them access to sedentary and hidden prey that are unavailable to iguanians. Iguanians rely on visual prey detection, and are ambush predators that capture mobile prey moving past ambush sites via lingual prehension.

Up to this point, we have adhered to the traditional historical scenario. As such, evolutionary shifts in use of sensory systems for prey detection and discrimination (visual versus chemical), prey prehension (lingual versus jaw), and activity levels (particularly as they translate into differences in foraging behavior), appear to tie in well with associated shifts in prey types and microhabitat use of lizards (see, for example, Pianka and Vitt, 2003; Vitt *et al.*, 2003). However, phylogenetic hypotheses are just that, mere hypotheses. A recent re-evaluation of squamate evolutionary history based on a combination of nuclear (*RAG-1* and *c-mos*) and mitochondrial (*ND2* region) genes suggests a very different pattern, one that is only partly consistent with our former findings (Townsend *et al.*, 2004). This phylogenetic hypothesis places Iguania and Autarchoglossa as sister

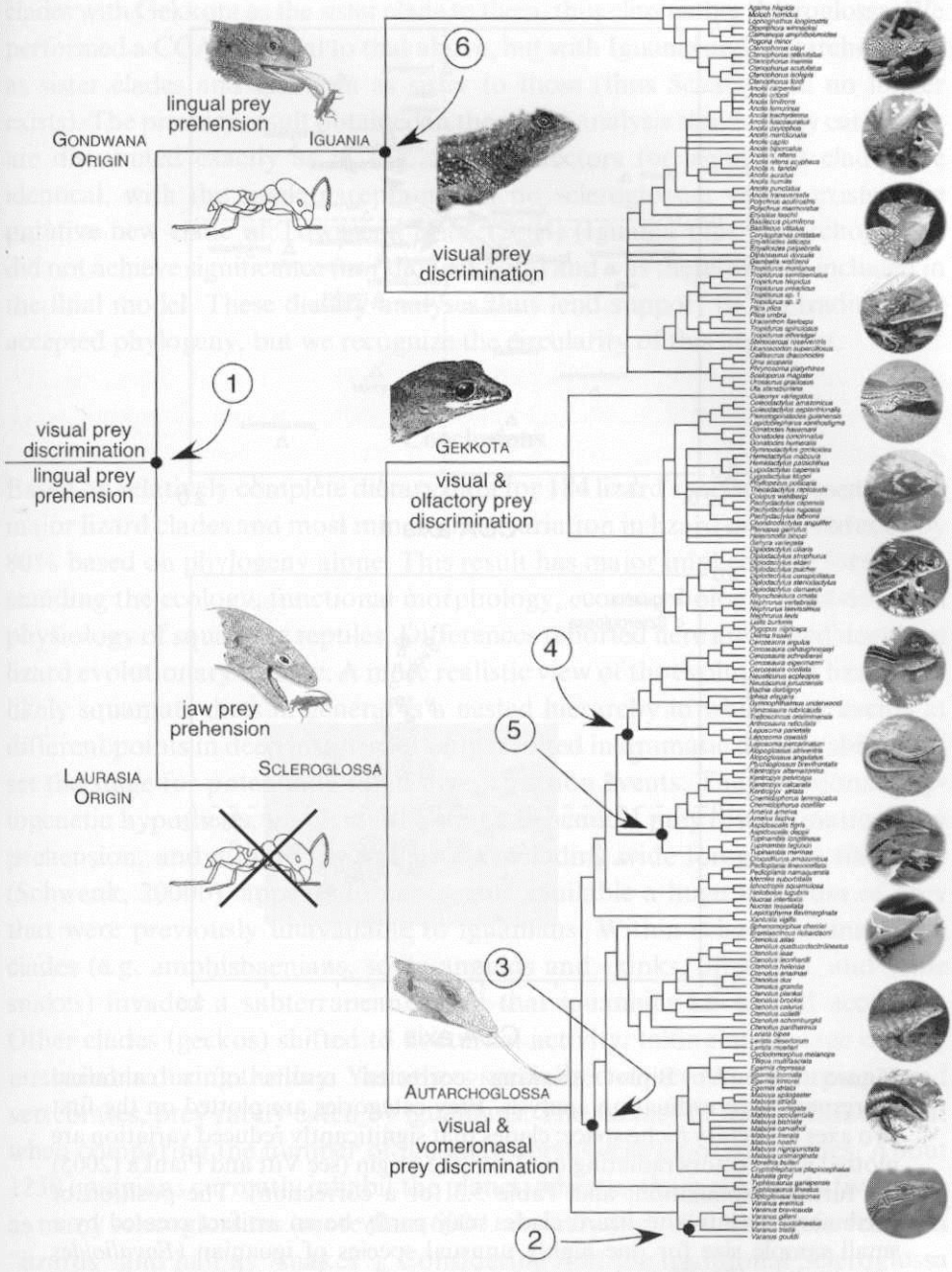

Figure 5.7. Phylogenetic hypothesis for 184 neotropical and desert lizard species. Solid circles indicate taxonomic groups that were significant in the CCA (1, Iguania/Scleroglossa; 2, Varanidae; 3, Scincidae; 4, Gymnophthalmidae; 5, Teiidae; 6, Iguanidae/Agamidae). Phylogenetic hypothesis is a composite based on published literature summarized by Vitt and Pianka (2005). Original version of figure, copyright 2005, National Academy of Sciences, USA.

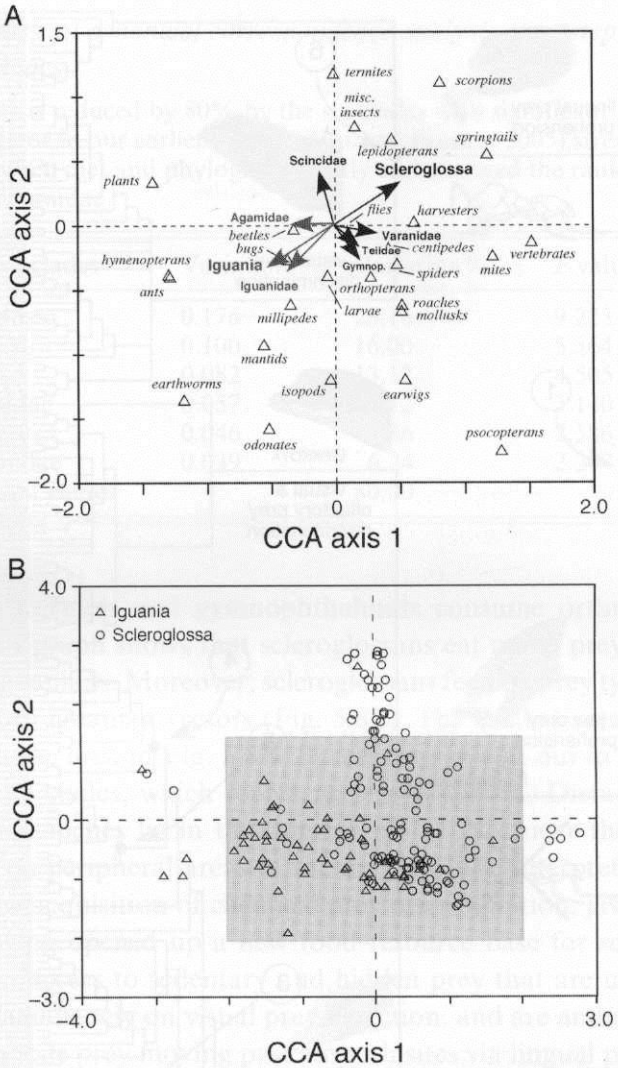

Figure 5.8. (A) Biplot showing corrected results of a canonical correspondence ordination analysis. Prey categories are plotted on the first two axes of dietary niche space; clades that significantly reduced variation are plotted with vectors radiating out from the origin (see Vitt and Pianka (2005) for further explanation, and Table 5.3 for a correction). The position of earthworms relative to lizard clades may partly be an artifact created by a small sample size for one highly unusual species of iguanian (*Enyalioides palpebralis*). (B) Plot showing positions of each species of iguanians (triangles) and scleroglossans (circles) in the first two CCA axes of dietary niche space. Original version of figures, copyright 2005, National Academy of Sciences, USA.

clades with Gekkota as the sister clade to them, thus eliminating Scleroglossa. We performed a CCA identical to that above, but with Iguania and Autarchoglossa as sister clades and Gekkota as sister to those (thus Scleroglossa no longer exists). The primary result obtained in the above analysis stands. Prey categories are distributed exactly as in Fig. 5.8 and vectors for significant clades are identical, with the single exception that no scleroglossan vector exists. The putative new clade of Townsend *et al.* (2004) (Iguania plus Autarchoglossa) did not achieve significance (nor did Gekkota) and was therefore not included in the final model. These dietary analyses thus lend support to the traditionally accepted phylogeny, but we recognize the circularity of this argument.

Conclusions

Based on relatively complete dietary data for 184 lizard species representing all major lizard clades and most minor ones, variation in lizard diets is reduced by 80% based on phylogeny alone. This result has major implications for understanding the ecology, functional morphology, ecomorphology, behavior, and physiology of squamate reptiles. Differences reported here are nested deeply in lizard evolutionary history. A more realistic view of the evolution of lizard and likely squamate diets in general is a nested hierarchy in which key events at different points in deep history not only resulted in dramatic dietary shifts, but set the stage for potentially rapid diversification events. The traditional phylogenetic hypothesis, involving the shift to chemical prey discrimination, jaw prehension, and a more active lifestyle including wide foraging to find prey (Schwenk, 2000b), appears to have made available a huge spectrum of prey that were previously unavailable to iguanians. Within scleroglossans, some clades (e.g. amphisbaenians, some anguids and skinks, dibamids, and some snakes) invaded a subterranean world that iguanians never had access to. Other clades (geckos) shifted to nocturnal activity, taking advantage of prey unavailable during the day. Yet others specialized on termites, scorpions, and vertebrates, prey rarely eaten by iguanians. The success of this shift is evident when comparing the number of iguanian versus scleroglossan species. About 1230 iguanians currently inhabit the planet, whereas there are nearly five times as many scleroglossans (more than 6000, about half of which are referred to as "lizards" and half as "snakes"). Considering that the traditional Scleroglossa and Iguania are equal ages (sister clades), this is a dramatic difference. However, because the divergence process is a Markovian process, the possibility exists that, dramatic as this difference is, it may have resulted from chance (see Vitt and Pianka, 2005). The striking ecological and morphological shifts that have occurred among scleroglossans but not iguanians

(nocturnality, multiple origins of limblessness and aquatic habits), adds support to the notion that historical traits of scleroglossans facilitated adaptive radiations and provided the basis for increased diversity.

Mechanistic studies of competition, evolutionary change in morphology in response to microhabitat structure, sexual selection, and thermoregulation and its correlates are best conducted among closely related species. Caribbean *Anolis* lizards, for example, have been ideal models for experimental field studies, likely because sympatric species share a vast majority of their evolutionary histories (Losos, 1992, 1994; Jackman *et al.*, 1999). Changes in response to other species or habitat change can be detected because species interactions between highly similar species are usually intense (see, for example, Losos *et al.*, 1997). Similar experiments performed on species embedded in different clades would be much less likely to detect measurable responses because deep historical differences mask characteristics of interest. Studies that seek to identify origins of differences among distantly related species or taxa require well-supported phylogenies and high-quality natural history data directed at the question of interest. Understanding foraging ecology of squamates, and likely of all organisms, requires identifying historical bases for differences among potentially interacting species in local assemblages if structure in natural communities is to be understood (see, for example, Losos, 1996; Webb *et al.*, 2002; Vitt *et al.*, 2003).

Clearly, predictions generated by early studies of foraging mode (e.g. Huey and Pianka, 1981) are not necessarily robust. Perhaps foraging mode should not be considered a paradigm, but rather an epiphenomenon that arose through the evolution of traits early in the history of squamate reptiles. Historical events need to be thoroughly examined in a phylogenetic context. Unfortunately, we do not have nearly the data necessary to do that. At best, we are just beginning to realize how important historical events are, yet the vast majority of research on lizards has been conducted on less than 10% of extant species. Recall that, for the Amazon assemblage of 19 species, 32.3% of the total dietary variation was explained by phylogeny. This assemblage is but a small subset of the 184 species. Poor taxon sampling strongly affects results. Considering that we can reduce variance by 32% with 19 species, but 80% with 184 species, imagine if we had all species! The "unexplained" variance in diets likely represents a combination of error due to poor taxon sampling, effects of species interactions, and other factors identified in this chapter.

Caveat

We have focused most of our analysis on 184 species from New and Old World deserts and New World tropics. Acquiring these data has taken both of our

lifetimes (we are not dead yet!). As in almost all studies that attempt "global" hypothesis testing, our data suffer from grossly inadequate taxon sampling. One-hundred eighty-four species may sound impressive, but it represents only 4.25% of "lizards" and 2.25% of squamates. Although some interesting patterns have been identified, alternative partitions of our dataset are possible. For example, clade representation is strongly dependent on region (i.e. South America, Central America, North America, Australia, Kalahari) (Table 5.4). Resources undoubtedly differ between deserts and tropical forests or savanna, and effects of predators on effective resource availability for squamates is likely quite different among habitat types as well. Clearly, more complete and robust phylogenetic hypotheses and much more dietary data from natural populations are needed to fully understand evolution of diets in squamate reptiles.

Table 5.4 *Numbers of species in various clades and families by geographic region*

SA, South America; CA, Central America; NA, North America; AU, Australia; K, Kalahari.

Clade	SA	CA	NA	AU	K	Tot
Iguania	27	11	8	11	1	58
Scleroglossa	49	5	3	49	20	126
Gekkota	13	2	1	13	7	37
Autarchoglossa	34	4	2	36	13	89
Scincomorpha	37	4	1	27	13	82
Anguimorpha	1	—	—	6	–	7
Family						
Agamidae	—	—		11	1	12
Anguidae	1	—	—		—	1
Diplodactylidae	—	—	—	11	—	11
Eublepharidae	—	—	1	—	—	1
Gekkonidae	13	1	–	2	7	23
Sphaerodactyline	7	—	—	–	—	7
Gekkonine	6	1	—	2	7	16
Gymnophthalmidae	19	—	—	—	—	19
Iguanidae	27	11	8	—	—	46
Lacertidae	—	—	—	—	7	7
Pygopodidae	—	—	—	3	—	3
Scincidae	5	2	—	27	6	40
Teiidae	12	1	1	—	—	14
Varanidae	—	—	—	6	—	6
Xantusidae	—	1	1	—	—	2
Totals (by family)	76	16	11	60	21	184

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